NEW AUSTRALIAN ALLODAPINE BEES (SUBGENUS *EXONEURELLA* MICHENER) AND THEIR IMMATURES (HYMENOPTERA: ANTHOPHORIDAE)

by T. F. HOUSTON*

Summary

HOUSTON, T. F. (1976).—New Australian Allodapine bees (subgenus *Exoneurella* Michener) and their immatures (Hymenoptera: Anthophoridae). *Trans. R. Soc. S. Aust.* **100**(1), 15-28, 28 February, 1976.

Three new species of *Exoneura* Smith (*E. eremophila*, *E. setosa* and *E. tridentata*) are described and figured. They are assigned to the formerly monotypic subgenus *Exoneurella* Michener and both adults and immatures of the new species are compared with those already described for the type-species, *E. lawsoni* Rayment. A key for identification of adults is provided.

Females of *E. tridentata* vary greatly in size and exhibit allometric variation of the head and metasoma.

Introduction

The chief purpose of this paper is to provide names for three species of bees whose ethology is to be dealt with in a subsequent work. An exhaustive examination of material from collections has not been attempted and the descriptions to follow are based on specimens in the collections of the author and the South Australian Museum.

The three new species are assigned to the subgenus *Exoneurella* Michener (of *Exoneura* Smith) which formerly contained only the type-species, *E. lawsoni* Rayment. Since *Exoneurella* was founded partly on the basis of the larval characteristics of *E. lawsoni*, it seemed of interest to describe and compare immatures of the new species. Generally, the characteristics of the new species support retention of *Exoneurella* as a discreet taxon.

The size-correlated variation of females of *E. tridentata* sp. nov. is detailed below as it is significant in terms of the bionomics of the species. Such variation is unusual amongst allodapine bees and in the family Anthophoridae as a whole.

The following abbreviations are used for the names of institutions and collections referred to in the text below: ANIC (Australian National Insect Collection, C.S.I.R.O., Canberra), HC (author's private collection, to be deposited in SAM), KU (Snow Entomological Museum, University of Kansas, Lawrence, Kansas, U.S.A.), SAM (South Australian Museum, Adelaide) and WADA (Western Australian Department of Agriculture, Perth).

Except where stated otherwise, all specimens listed in this paper were collected by the author.

Genus EXONEURA Smith

Exoneura Smith, 1854, p. 232. See Michener, 1965, pp. 223-226 for detailed description, subgenera and species.

Subgenus EXONEURELLA Michener

Exoneurella Michener, 1963, p. 257 (erected as a genus); 1965, pp. 223-224 (relegated to subgeneric status; diagnosis provided).

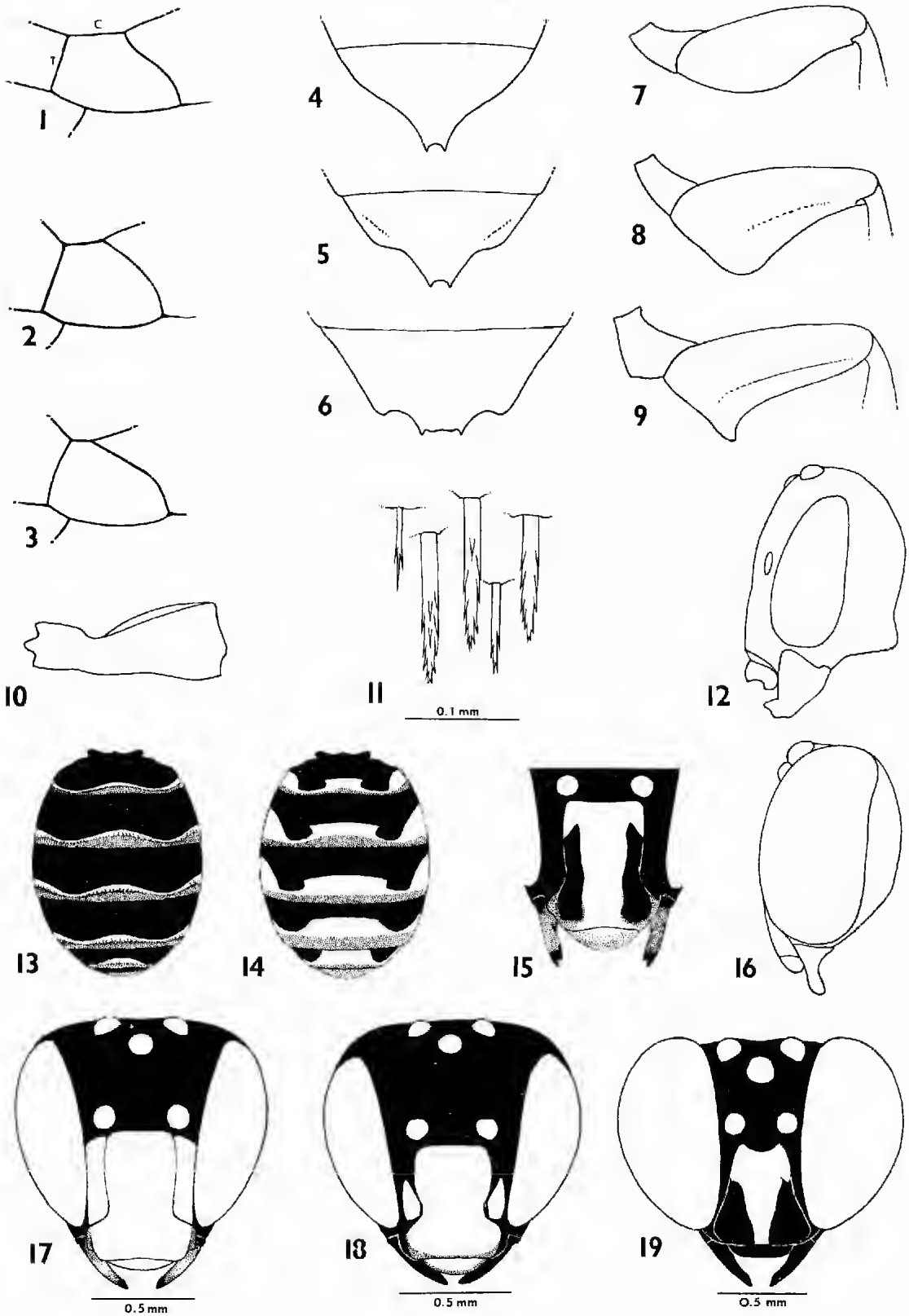
THE ADULTS

Key to the species of Exoneurella

1. Second cubital cell of fore wing with subequal costal and medial borders (Fig. 1); 6th metasomal tergum of female with simple non-bifid apex and a pair of lateral projections (Fig. 24, 25); compound eyes of male strongly swollen (Fig. 19) ..... *E. tridentata*

1. Second cubital cell of fore wing with costal margin conspicuously shorter than medial margin (Figs 2, 3); 6th metasomal tergum of female with bidentate apex and with or without lateral

* South Australian Museum, North Terrace, Adelaide, S. Aust. 5000.



FIGS 1–19

projections (Figs 4–6); compound eyes of male not swollen (Figs 17, 18) 2

2. Sixth metasomal tergum of female without lateral prominences, margins smoothly sinuate (Fig. 4); hind femora of male obtusely produced and carinate ventrally (Fig. 8); metasomal terga of both sexes black without cream or creamy-brown pigmentation and without numerous conspicuously thickened setae ..... *E. lawsoni*

2. Sixth metasomal tergum of female with distinct lateral projections or prominences (Figs 5, 6); hind femora of male unmodified (Fig 7) or not modified as in Fig. 8; metasomal terga of both sexes with faint to distinct cream bands; terga 3 and 4 (females) or 4 and 5 (males) with numerous conspicuously thickened setae (Fig. 11) 3

3. Metasomal terga yellow-brown to black with wide cream bands (Fig. 14); 6th metasomal tergum of female with subacute lateral projections (Fig. 6); hind femora of male each with an acute ventral projection (Fig. 9) ..... *E. eremophila*

3. Metasomal terga largely black with narrow (sometimes faint or incomplete) cream subapical bands (Fig. 13); 6th metasomal tergum of female with very obtuse lateral prominences (Fig. 5); hind femora of male unmodified (Fig. 7) ..... *E. setosa*

Exoneura (Exoneurella) eremophila n.sp.

Figs 2, 6, 9, 14, 15, 17

Types

Holotype: ♂ (SAM, 1 20961), New Kalamurina Homestead, S. Aust. (27°44'S, 138°15'E), 9–11.iii.1972, on *Wahlenbergia*.

Allotype: ♀ in SAM. Paratypes: 42 ♂, 44 ♀ in SAM; 2 ♂, 2 ♀ in ANIC; 1 ♂, 1 ♀ in KU.

Diagnosis: This species differs from all other *Exoneurella* as follows. Lateral face marks of male filling spaces between clypeus and compound eyes (Fig. 17); metasomal terga of both sexes yellow-brown to black with extensive cream maculations (Fig. 14); pronotum with a pair of cream marks sublaterally; hind femora of male each with an acute ventral projection (Fig. 9); 6th metasomal tergum of female with bidentate apex and a pair of subacute lateral projections (Fig. 6).

Description

Male. Body length 3.8–4.1 mm; head width 1.1–1.2 mm.

Head capsule as broad as long; compound eyes of usual relative size (Fig. 17); face narrowed to about 43% of head width; ocelli approximately equal in size to antennal sockets; scapes failing to reach level of median ocellus; flagella 85% as long as head width, the middle segments about as long as broad; genae viewed laterally almost half as wide as compound eyes and evenly convex; fore legs not especially slender, the fore tibiae about 3.5x as long as wide; hind femora laterally compressed, each with an acute ventral projection (Fig. 9); costal margin of 2nd cubital cell of fore wing about half as long as 1st transverse cubital vein (Fig.2).

Integument glossy generally with sparse fine pitting or none; metasomal terga very finely lineate.

Pubescence white, virtually absent dorsally but fairly long and dense ventrally and on legs and mesepisterna; 4th and 5th metasomal terga (except laterally) with a sparse covering of thickened bristle-like setae.

The following areas white or cream: lower face, labrum and middle portions of mandibles (Fig. 17), scapes and pedicels ventrally, tubercles and dorsal margin of pronotum (except medially), spots on tegulae, basal parts of wing veins, subapical bands on metasomal terga (Fig. 14), apices of femora, bases of tibiae, anterior edges of fore tibiae, and basitarsi. The following areas yellow-brown: scapes dorsally, flagella ventrally, most parts of legs (except for cream areas), metasoma

---

Figs 1–3. Second cubital cells of right fore wings (in dorsal views) of *Exoneura* (*Exoneurella*) *tridentata*, *E.* (*E.*) *eremophila*, and *E.* (*E.*) *setosa* respectively. C = costal margin, 1 = first transverse cubital vein.

Figs 4–6. Sixth metasomal terga (dorsal views) of females of *E.* (*E.*) *lawsoni*, *E.* (*E.*) *setosa* and *E.* (*E.*) *eremophila* respectively.

Figs 7–9. Trochanters, femora and apices of tibiae of left hind legs (anterior views) of males of *E.* (*E.*) *setosa*, *E.* (*E.*) *lawsoni* and *E.* (*E.*) *eremophila* respectively.

Fig. 10. Left mandible of female of *E.* (*E.*) *tridentata* (ventral view).

Fig. 11. Thickened bristle-like setae from fourth metasomal tergum of female of *E.* (*E.*) *setosa*

Fig. 12. Head capsule of a relatively large female of *E.* (*E.*) *tridentata* (left lateral view).

Figs 13 and 14. Metasomae (dorsal views) of males of *E.* (*E.*) *setosa* and *E.* (*E.*) *eremophila* respectively showing cream bands (white) and translucent tergal margins (stippled).

Fig. 15. Lower portion of head of female of *E.* (*E.*) *eremophila* (anterior view) showing T-shaped clypeal mark.

Fig. 16. Head capsule of male of *E.* (*E.*) *tridentata* (left lateral view).

Figs 17–19. Head capsules (anterior views) of males of *E.* (*E.*) *eremophila*, *E.* (*E.*) *setosa* and *E.* (*E.*) *tridentata* respectively.

ventrally and partially or extensively dorsally. Remaining areas black or dark brown.

Female. Body length 4.0–5.5 mm; head width 1.1–1.2 mm.

Head form similar to that of male (Fig. 17); flagella about 67% as long as head width; mandibles tridentate but not constricted subapically; metasoma fairly elongate; 6th metasomal tergum with a bidentate apex and a pair of small but almost acute upturned lateral projections (Fig. 6); hind femora unmodified.

Integument and pubescence much as in male but thick bristle-like setae occur only on terga 3 and 4.

Coloration as in male except that white on face is limited to a full-length T-shaped mark on clypeus (Fig. 15).

Variation

The extent of yellow-brown coloration on the metasoma varies considerably amongst individuals collected together and some specimens have creamy-brown maculations on the lateral margins of the scutum and scutellum.

The specific name, derived from Greek, means loving solitude and alludes to the arid habitat of the species.

Distribution

Central regions of Australia including portions of the Northern Territory, Queensland, New South Wales and South Australia.

Specimens examined: The holotype and the following. *QLD.*: 9 ♂, 8 ♀, 3 miles (4.8 km) W. of Windora, 17.iv.1969, ex nests (HC). *N.S.W.*: 1 ♀, 82 miles (132 km) W. of Cobar, 31.i.1971, on *Ptilotus* (SAM); 1 ♂, 14 ♀, 70 miles (113 km) E. of Wilcannia, 31.i.1971, on *Helichrysum*, *Goodenia* and *Wahlenbergia* (SAM). *S. AUST.*: 1 ♀, Amata (Musgrave Park) settlement, 14.x.1972, on *Calandrinia*, *H. E. Evans & T. F. Houston* (SAM); 1 ♀, 33 miles (53 km) W. of Amata, 17.x.1972, ex nest in pithy twig, *H. E. Evans & T. F. Houston* (SAM); 7 ♀, Bettys Well (132°26'E, 27°2'S), Everard Park Stn, 1–5.xi.1970, on *Hibiscus farragei* (SAM); 45 ♂ (paratypes), 48 ♀ (allotype and paratypes), New Kalamurina HS, (27°44'S, 138°15'E), 9–11.iii.1972, on *Wahlenbergia* (7 ♂, 5 ♀ pinned), ex dead stems of *Myriocephalus* (38 ♂, 43 ♀ in alcohol) (ANIC, KU, SAM); 2 ♀, Morgan, 19.xii.1963, on *Wahlenbergia* (HC); 4 ♂, 4 ♀, 10 miles (16 km) S. of Mt Davies airstrip, 21.x.1972, on *Ptilotus*, *H. E. Evans & T. F. Houston* (SAM); 2 ♀, Mt Miccollo (32°31'S, 136°36'E), Siam Stn, 20.iv.1971, ex nest (SAM); 1 ♀, S. of Tomkinson Ranges (129°8'E, 26°10'S), 18.x.1972, on *Scaevola*, *H. E. Evans & T. F. Houston* (SAM); 2 ♀, 31 miles (50 km) W. of Welbourn Hill HS, 13.x.1972, on blue *Eremophila*, *H. E. Evans & T. F. Houston* (SAM); 2 ♀, 10 miles (16 km) SE. of William Creek, 28.x.1972, on *Hakea*, *H. E. Evans & T. F. Houston* (SAM).

Exoneura (Exoneurella) lawsoni Rayment, 1946, pp. 230-232, fig. 2 (male, not female or larva).

FIGS 4, 8

Exoneurella lawsoni (Rayment) Michener, 1963, p. 257.

Exoneura (*Exoneurella*) *lawsoni* Rayment. Michener, 1965, p. 224.

Holotype: ♂ (in ANIC), Canberra, A.C.T., Newton R. Lawson, July 1945.

I have not examined the holotype but Ms Josephine Cardale (ANIC) made a critical examination of it on my behalf and confirmed that it agrees with the male characteristics given in the diagnosis below.

Michener (1963, p. 258) pointed out that the females and larvae described by Rayment in the original description of *E. lawsoni* are of another species and are referable to the subgenus *Brevineura*.

Diagnosis: E. lawsoni differs from all other *Exoneurella* as follows. Hind femora of male carinate and broadly produced ventrally (Fig. 8); 6th metasomal tergum of female lacking lateral prominences, the margins gently sinuate (Fig. 4). Differs from *E. setosa* and *E. eremophila* in complete absence of cream pigmentation from metasoma and in absence (or only feeble development) of thickened bristle-like setae on dorsum of metasoma.

For a detailed description of both sexes see Michener (1963, p. 259). Note, however, that the pale maculations of the face of the male are white, not pale yellow.

Distribution: On and near Great Dividing Range of south-eastern Queensland, New South Wales and eastern Victoria.

Specimens examined: QLD.: 4 ♂, 5 ♀, Bunya Mountains, 8.x.1968, ex nests (HC). *VIC.*: 1 ♂, 2 ♀, Tambo Valley, 22.i.1966, on *Wahlenbergia* (HC).

Exoneura (Exoneurella) setosa n.sp.

FIGS 3, 5, 7, 11, 13, 18

Types

Holotype: ♂ (SAM, I 20962), West Beach, Adelaide, S. Aust., 25.iv.1975, ex dead *Euphorbia* stem, C. A. & T. F. Houston.

Allotype: ♀ in SAM. Paratypes: 7 ♂, 10 ♀ in SAM; 4 ♂, 4 ♀ in ANIC; 2 ♂, 2 ♀ in KU.

Diagnosis: Very like *E. lawsoni*, differing as follows. Hind femora of male unmodified, lacking ventral flanges and projections (Fig. 7); 6th metasomal tergum of female with a pair of lateral convexities (Fig. 5); metasomal terga of both sexes with narrow subapical bands of creamish pigment (sometimes faint or incomplete, especially medially) and trans-

lucent brown apical margins (Fig. 13); metasomal terga 4 and 5 (male) or 3 and 4 (female) with numerous conspicuously thickened, bristle-like setae (Fig. 11).

Description

Male. Body length 3.8–4.7 mm; head width 1.1–1.2 mm.

Head capsule 1.1x as broad as long; compound eyes of usual size (Fig. 18); face narrowed to about 42% of head width in lower part; ocelli approximating size of antennal sockets; scapes just failing to reach level of median ocellus; flagella about 72% as long as head width; middle flagellar segments slightly broader than long; genae viewed laterally 2/3 as wide as compound eyes and evenly convex; fore legs not unusually elongate, the fore tibiae about 3.5x as long as wide; hind femora unmodified (Fig. 7); costal margin of 2nd cubital cell of fore wing about 1/4 to 1/2 as long as 1st transverse cubital vein (Fig. 3).

Integument almost entirely glossy; clypeus and scutellum finely pitted; dorsal area of propodeum dulled by extremely fine sculpturing; metasomal terga finely lineate.

Pubescence white, sparse on head and body, densest laterally and ventrally on thorax and basal parts of legs; 4th and 5th metasomal terga with numerous short but thick bristle-like setae (Fig. 11) on dorso-apical areas.

The following areas white: almost all of clypeus and a spot of variable size on each side (Fig. 18), labrum, anterior stripe on fore tibia, spots at bases of mid and hind tibiae, pronotal tubercles and alar sclerites. The following areas off-white to cream: ventral edges of scapes, mid and hind basitarsi, narrow subapical bands on metasomal terga (Fig. 13; sometimes faint or incomplete especially medially). Fore legs (largely) and mid femora and tibiae anteriorly yellow-brown. Hind margins of metasomal terga translucent pale brown; remaining areas black or blackish brown.

Female. Body length 4.3–5.5 mm; head width 1.1–1.2 mm.

Head form similar to that of male; flagella 64% as long as head width; mandibles tridentate but not constricted subapically; metasoma elongate, the 6th tergum with bidentate apex and a pair of obtuse lateral prominences (Fig. 5).

Integument sculptured as in male.

Pubescence much as in male but bristle-like setae occur on hind margin of 3rd metasomal tergum and dorsal area of 4th.

Coloration differs from that of male as follows: clypeus with a full-length white T-shaped stripe; paraocular areas without white spots; labrum entirely brownish; legs lacking yellow-brown coloration.

The specific name, derived from Latin and meaning 'bristly', alludes to the setation of the metasoma.

Distribution

Lowlands of southern South Australia (west to Spencer Gulf) and of south-eastern Queensland.

Specimens examined: The holotype and the following, *QLD*: 1 ♀, 2 miles (3.2 km) S. of Nanango, 7.x.1968, on *Wahlenbergia* (HC); 1 ♂, 3 ♀, 3 miles (4.8 km) N. of Peregian Beach (near Noosaville), 9.xii.1966, ex nests (HC). *S. AUST.*: 2 ♂, 5 ♀, Glenelg North (dunes), Adelaide, 24.x.1963, 6.xii.1964 and 14-16.i.1965, on pigface and *Wahlenbergia* flowers (HC); 1 ♀, Mambray Creek Rail Siding, 13.xi.1970, ex pithy stem (SAM); 3 ♀, Morgan, 18–19.xii.1963, on *Wahlenbergia* (HC); 13 ♂ (paratypes), 17 ♀ (allotype and paratypes), West Beach, Adelaide, same data as for holotype (ANIC, KU, SAM); 4 ♂, 3 ♀, West Beach, Adelaide, 5 and 24.ii.1965, 27.ix.1965, on *Wahlenbergia* and ex hollow stems (HC).

Exoneura (Exoneurella) tridentata n. sp.

FIGS 1, 10, 12, 16, 19-30

Types

Holotype: ♂ (SAM, I 20963), Lake Gilles National Park (136°46'E, 33°2'S), S. Aust., 31.xii.1973, ex short tunnel in twig of *Heterodendron*.

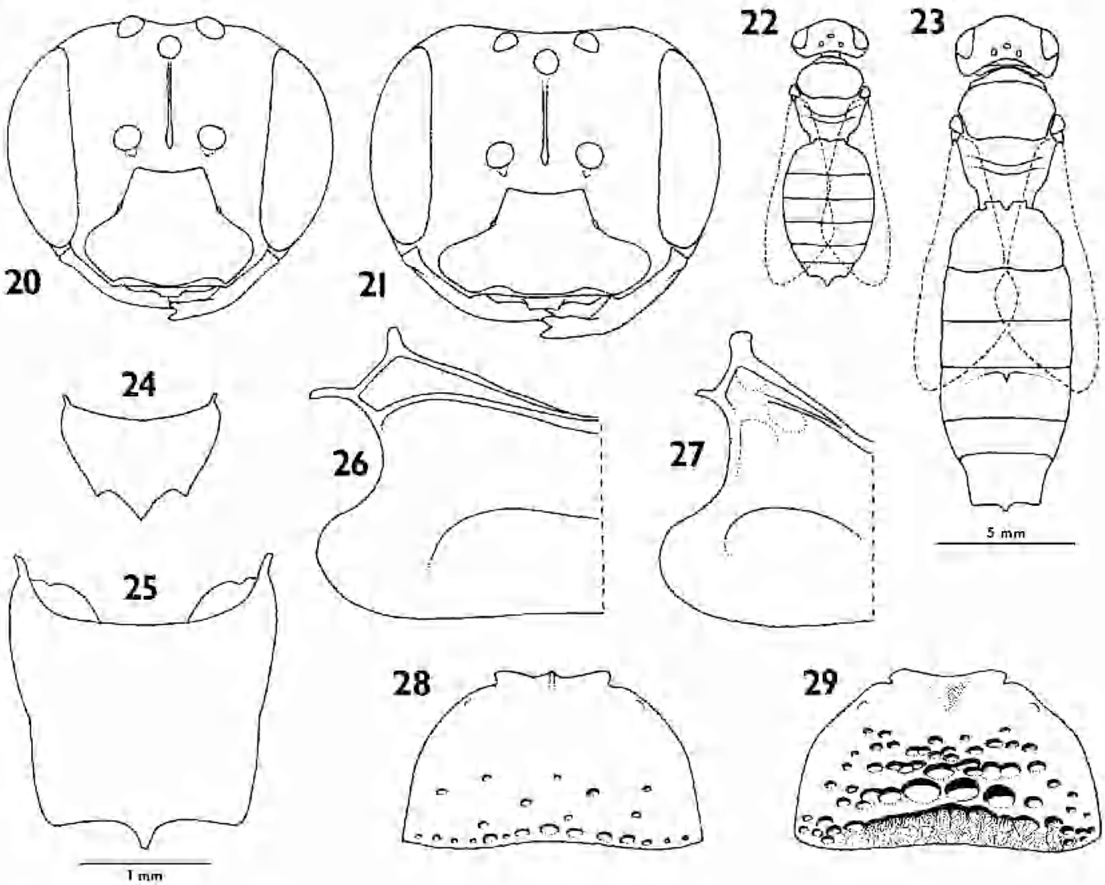
Allotype: ♀ in SAM. Paratypes: 39 ♂, 29 ♀ in SAM; 2 ♂, 5 ♀ in ANIC; 1 ♂, 2 ♀ in KU.

Diagnosis: E. tridentata differs from all other *Exoneurella* as follows. Costal margin of 2nd cubital cell of fore wing equal to or slightly longer than 1st transverse cubital vein (Fig. 1); scapes reaching to above level of median ocellus; male with swollen compound eyes and relatively narrow face (Fig. 19) and fore legs conspicuously elongated; female with angular genae (Fig. 12), mandibles constricted subapically (Fig. 10) and 6th metasomal tergum with non bifid apex (Figs 24, 25).

Description

Male. Body length 4.5–4.9 mm; head width 1.6–1.9 mm.

Head capsule 1.3x as broad as long; compound eyes strongly swollen so that face appears sunken between them; face narrowed to about 1/4 of head width (Fig. 19); ocelli relatively large (about 1.4x as wide as antennal sockets); genae viewed laterally (Fig. 16) much narrower than compound eyes and not angular; scapes slender, reaching to just above



Figs 20–29. *Exoneura* (*Exoneurella*) *tridentata* female. Figs 20, 21.—Head capsules (anterior views) of smallest and largest known specimens respectively, drawn to same length. Figs 22, 23.—Smallest and largest known specimens respectively (dorsal views) (antennae and legs omitted, fore wings represented by broken lines). Figs 24, 25.—Sixth metasomal terga (dorsal views) of smallest and largest known specimens, respectively. Figs 26, 27.—Left halves of fourth metasomal sterna (dorsal views) of smallest and largest known specimens, respectively, drawn to same length. Figs 28, 29.—First metasomal terga (dorsal views) of smallest and largest known females, respectively, drawn to same size to illustrate differences in surface pitting.

level of median ocellus; flagella relatively short, 1/2 as long as head width, all segments but apical one broader than long; fore legs very slender, the tibiae 5x longer than wide; hind femora unmodified; costal margin of 2nd cubital cell of fore wing equal to or longer than 1st transverse cubital vein (Fig. 1); metasoma relatively short, broad and depressed.

Integument of face smooth but dull with close small pitting on clypeus; scutum and scutellum glossy with very sparse fine pitting; mesepisterna dulled by shallow coarse pitting; anterior half of 1st metasomal tergum glossy and impunctate, the posterior half and most of tergum 2 pitted and finely roughened, dull except laterally; tergum 3 shiny but coarsely pitted; terga 4 to 7 duller with fine reticulate sculpture.

Pubescence white, fairly long and sparse generally, densest on clypeus, posterior of head, sides and venter of thorax, sides of propodeum, basal areas of legs and 1st metasomal tergum.

Colour black generally except for the following: clypeal mark (Fig. 19), ventral edges of scapes, patches on tegulae and wing bases and spot at base of each tibia white to cream; apical portions of femora, all tibiae and tarsi orange-brown; wing veins and ventral surfaces of flagella brown.

Female. Size extremely variable; body length 4.8–10.0 mm; head width 1.3–2.1 mm.

Head (viewed anteriorly) grading from fairly round in small females (Fig. 20) to rather quadrate in large females (Fig. 21); accordingly the inner orbits vary from slightly converging to slightly diverging below; genae (viewed laterally) almost as wide as compound eyes and very angular, especially in large specimens (Fig. 12); scapes slender and reaching median ocellus; flagella 65% as long as head width; labrum with a stout carinate median tubercle; mandibles tridentate, strongly constricted subapically (Fig. 10); legs not as slender as those of male; metasoma elongate and rather parallel-sided, more so in large females (Figs 22, 23); 6th tergum upturned, slightly to strongly concave dorsally, rather triangular with small lateral projections in small females (Fig. 24) grading to quadrate in large females (Fig. 25).

Integument largely glossy with few scattered small pits; dorsal and lateral areas of propodeum dull with fine roughening; 1st metasomal tergum of small specimens with relatively few pits concentrated along posterior margin (Fig. 28), of larger specimens with numerous coarser pits some of which exceed the ocelli in size and many of which coalesce to form an irregular emargination posteriorly (Fig. 29); more apical terga with sparse medium pitting and fine reticulate sculpturing, strongest on terga 4 to 6. Pubescence generally sparse, white and inconspicuous, longest on sides of metasoma and hind tibiae; dorsal areas of metasomal terga lacking thickened or conspicuous setae.

Head and body black; clypeus with a full length T-shaped white mark; labrum, mandibles and legs largely or wholly orange-brown; medium and large females usually have diffuse orange-brown patches on mesepisterna, metasternum and anterior metasomal sterna.

The specific name refers to the 3-pointed margin of the 6th metasomal tergum of the female.

Distribution

Semi-arid regions of South Australia and southern Western Australia (the mallee *Eucalyptus* belt and bordering areas).

Specimens examined: The holotype and the following. *S. AUST.*: 1 ♂ and 14 ♀ (all paratypes), Corunna Hills, N. of Iron Knob, 19.iv.1971, ex nest (SAM); 4 ♀, S. of Iron Baron, Eyre Peninsula, 30.xi.1971, on *Eremophila* (HC); 40 ♂ (paratypes), 26 ♀ (including allotype and 22 paratypes), Lake Gilles National Park, 30–31.xii.1973, 11–16.iv.1974, 14–17.vi.1974, 29.viii–1.ix.1974 and 27.x.1974, ex nests in hollow *Heterodendron* twigs, *C. A. & T. F. Houston* (ANIC, HC, KU and SAM —some in alcohol); 1 ♂ (paratype), 3 ♀, northern Middleback Ranges (137°9'E, 33°3'S), 7–8.x.1973, ex hollow *Heterodendron* twigs, *C. A. & T. F. Houston* (HC, SAM); 7 ♀, 8 miles (13 km) E. of Poochera, 8.i.1970, on *Melaleuca pubescens* (HC); 1 ♀, 29 km NNW. of Pt Augusta, 29.ix.1972, on *Myoporum* (SAM); 3 ♀, 2 miles (3.2 km) N. of Port Germein, 7.i.1970, on *Loranthus miraculosus* and *Melaleuca pubescens* (HC); 1 ♀, 30 miles (48 km) NNW. of Renmark, 22.i.1972, on mallee *Eucalyptus* (SAM). *W. AUST.*: 1 ♂, 27 miles (43 km) W. of Coolgardie, 18.i.1970, on *Eucalyptus* (HC); 1 ♀, 25 miles (40 km) E. of Kalbarri, 6.iii.1974, *K. T. Richards* (WADA); 1 ♀, 8 miles (13 km) S. of Wanoo, 7.v.1974, *K. T. Richards* (WADA).

Size-correlated variation in E. tridentata

As noted in the above description, females of *E. tridentata* vary markedly in size and form and slightly in coloration. Some of this variation is correlated with size and since it is significant in terms of the bionomics of the bees it is detailed below.

Individual size has been judged according to head capsule width. Measurements of fore wing lengths were made but proved unnecessary since the ratio of fore wing length to head width remained approximately constant over a range of measurements.

With increasing size, the following changes occur.

(1) The head capsule becomes increasingly more quadrate, the inner orbits changing from slightly converging to slightly diverging below and the clypeus becoming wider relative to its length (cf. Figs 20, 21).

(2) The metasoma becomes relatively larger (especially in length). In the smallest females the apex of the metasoma does not extend beyond the tips of the reflexed fore wings whereas in the largest females it protrudes beyond them by about 1/3 of its length (cf. Figs 22, 23). This increase in relative size is not due to extension of the telescopic segments but reflects an increase in size of all the component parts including the sting.

(3) The latero-apical projections of the 6th metasomal tergum become relatively larger, more obtuse and further apart (cf. Figs 24, 25). This variation is quantified in Figure 30.

(4) The 1st metasomal tergum becomes increasingly more coarsely and deeply pitted and in the larger females the pits along

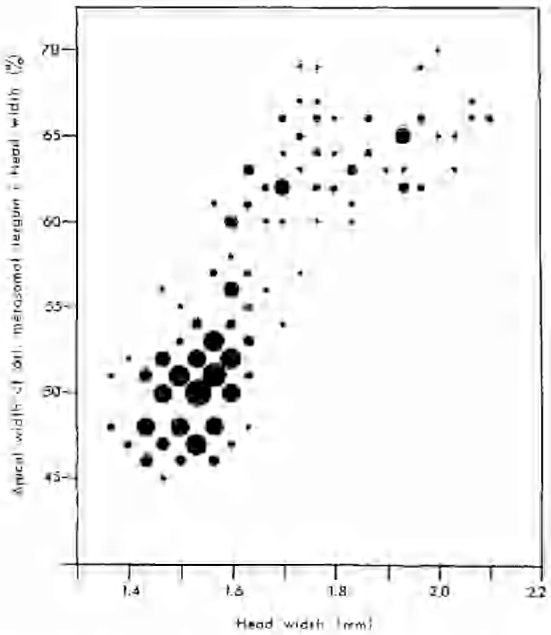


Fig. 30. Allometry in females of *Exoneura* (*Exoneurella*) *tridentata*. Scatter diagram showing how relative width of apex of sixth metasomal tergum increases with size of individual. The number of individuals represented by spots increases with their size in the order 1, 2, 3, 4, 5, 6–10, 11–15, 16–20 and 21–25.

the posterior margin coalesce to form an irregular emargination (cf. Figs 28, 29).

(5) The integument of the metasoma becomes relatively thicker and more brittle and the apodemes become relatively larger (cf. Figs 26, 27). The sturdier anterolateral apodemes are associated with relatively larger extensor muscles.

(6) Orange-brown patches with diffuse borders appear on the thorax and metasoma of medium and large females. They occur on the mesepisterna, mesosterna and anterior metasomal sterna. The larger the individual, the more extensive are the maculations.

(7) A small median spine develops from the gradulus of the 4th metasomal tergum in medium and large females.

This variation appears to be unique amongst allodapine bees and in the family Anthophoridae as a whole. Michener (1965*a*) discussed size variation amongst females of the social Australian bee, *Exoneura* (*E.*) *variabilis* Rayment. In this species, egg layers average larger than workers but no structural differences or allometry has been reported. The degree of size variation in this species is also less than in *E. tridentata*, the largest known females having head widths only 1.28x as great as the smallest females (cf. 1.54x in *E. tridentata*).

THE IMMATURES

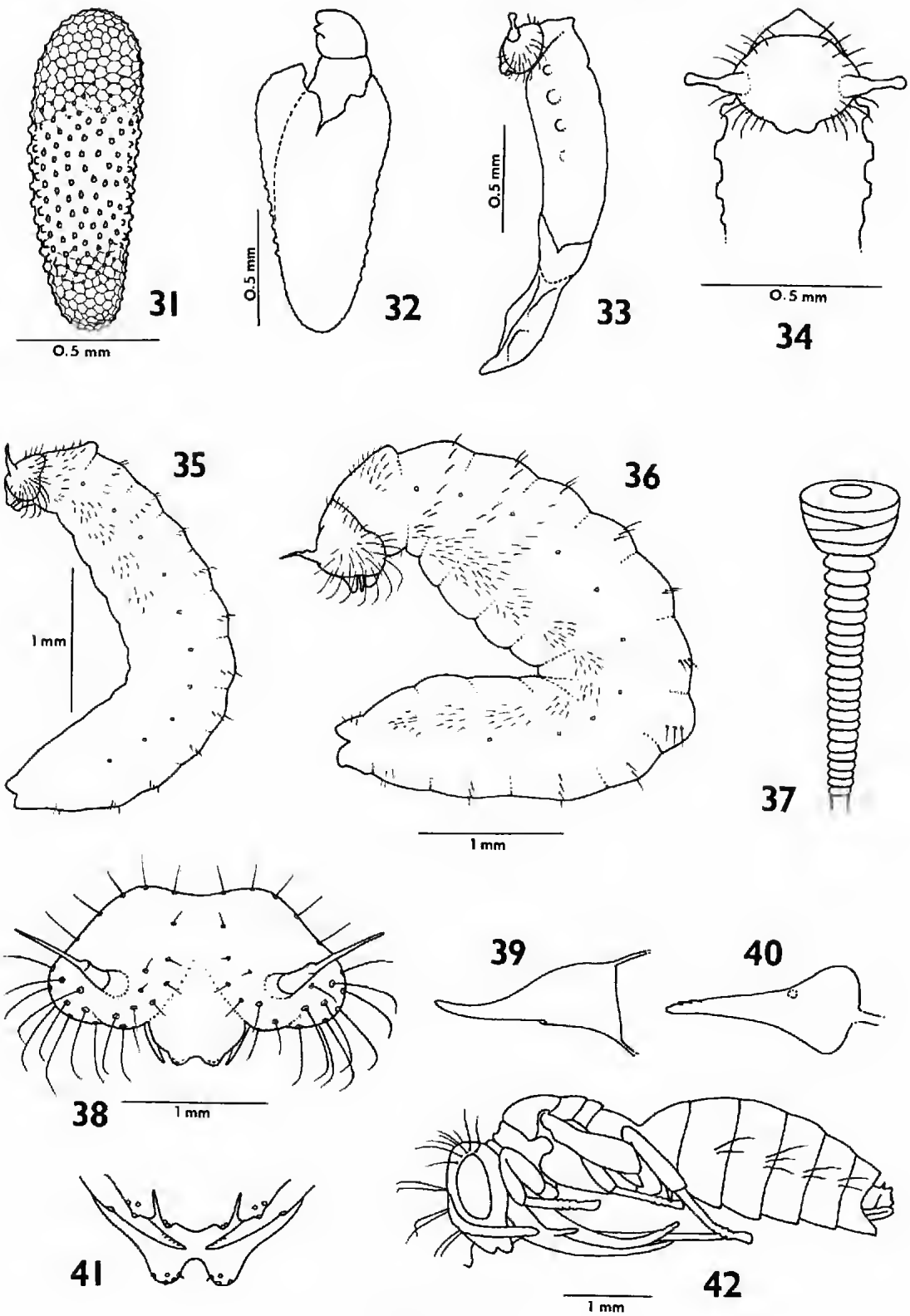
The immatures studied were preserved by dropping them live into either Kahle's solution or 75% ethyl alcohol and were stored in the latter.

Syed (1963) described 4 larval instars of *E. lawsoni* from preserved material and Michener (1964) described and figured live specimens of probable 2nd, 3rd and 4th instars as well as the egg, prepupa and pupa. However, the identity of the material studied and described by these authors is subject to a little uncertainty because a few of the nests from which it was derived have proven to belong to *E. setosa* (C. D. Michener—personal communication). Professor Michener confirms that the bulk of the adult material on which he based his 1964 studies is clearly *E. lawsoni* and in all probability the immatures described by him would be of the same species.

Four morphologically distinct larval instars can be recognised in each of the known species of *Exoneurella* without recourse to histograms of head width frequencies. Indeed, with *Exoneura tridentata* there is such marked size variation within each instar and such wide overlap in size between them that the histogram of head width frequencies was of no help at all in determining the number of instars.

The terminology employed in the following descriptions of larvae follows that of Michener (1953).

Figs 31–42. Immatures of *Exoneura* (*Exoneurella*) *eremophila*. Fig. 31.—Egg. Fig. 32.—First instar partly enclosed in chorion (left lateral view). Fig. 33.—Second instar with chorion still attached (left lateral view). Fig. 34.—Ventral view of head and fore body of second instar. Figs 35, 36.—Third and fourth instars, respectively (left lateral views). Fig. 37.—spiracle of fourth instar. Fig. 38.—Head of fourth instar (anterior view). Figs 39, 40.—Left mandible of fourth instar, anterior and ventral views, respectively. Fig. 41.—Mouthparts of fourth instar (posterior view). Fig. 42.—Female pupa (left lateral view).


31
0.5 mm
32
0.5 mm
33
0.5 mm
34
0.5 mm
35
1 mm
36
1 mm
37
38
1 mm
39
40
41
42
1 mm

FIGS 31–42

E. (E.) eremophila

Egg. (Fig. 31). About 1.1 mm long and 0.4 mm in maximum width; white, sausage-shaped and with a coarse reticulate sculpturing each end, the middle portion being tuberculate.

In some eggs from Queensland nests the sculpturing was weak or absent.

First instar.—(Fig. 32). Remains almost wholly within chorion; head of very simple form, lacking lateral lobes, antennae and setae; mouthparts hardly developed, lobe-like and probably non-functional; body sac-like without obvious segmental lines, tubercles or setae.

Second instar.—(Figs 33, 34). Chorion remains attached to abdomen; head relatively broader than in 1st instar but with no obvious lateral lobes; antennae well-developed, capitate and laterally directed; mouthparts well-developed and functional; head capsule with numerous moderately long setae; body without setae and distinct segmental lines but with 4 tubercles each side anteriorly and a middorsal tubercle on prothorax.

Third instar.— (Fig. 35). Entirely free of chorion; head relatively very broad with well developed ventrolateral lobes; antennae very slender and acute apically; body gently curved with distinct intersegmental lines, no anterolateral tubercles or ventrolateral swellings but prothorax with a distinct middorsal tubercle; anal slit moderately deeply incised; setae numerous on head and body, longest on ventrolateral lobes of head; patches of small setae occur dorsally and laterally on the prothorax, laterally on the following 4 segments and transverse rows of short stiff setae occur dorsolaterally on the 2nd to 12th body segments.

Fourth instar.—(Figs 36-41). Head relatively very broad with conspicuous ventrolateral swellings and slender acute antennae (Fig. 38); labrum bilobed apically with a few sensoria, not delimited from distinctly sunken clypeal region; mandibles slender apically with only a few minute spines subapically and a single sensorium ventrally (Figs 39, 40); maxillae shorter than labium, their palpi consisting of indistinct tubercles bearing a few sensoria (Fig. 41); labium bearing tubercle-like palpi latero-apically; body strongly bent at 5th abdominal segment (Fig. 36); prothorax with an obtuse mid-dorsal tubercle; intersegmental lines weak; ventrolateral body swellings absent; terminal segment of abdomen strongly laterally compressed with anal slit deeply incised; setation much as in 3rd instar but all body segments have ventrolateral patches of setae; atrial and primary tracheal openings of spiracles circular; atria without spines but with a few branching and anastomosing sculptural lines; subatria relatively long (Fig. 37).

Prepupa.—Similar to 4th instar except that the body is straight and swollen anteriorly.

Pupa.—(Fig. 42). Conforms essentially to features of the adult but the following special pupal structures were noticed: all coxae with ventro-apical spines (very short and inconspicuous on mid and hind coxae of females); vertex (across full width), interantennal area, upper, middle and lower clypeus with extremely long setae; 2nd to 5th metasomal segments also with 2 or 3 long setae each side; in some specimens the more apical metasomal terga bear a few tiny setae dorsally.

Material examined.—155 eggs, 109 larvae and prepupae and 46 pupae, New Kalamurina HS, S. Aust., 9–11.iii.1972, ex dead stems of *Myriocephalus;* 7 eggs, 48 larvae and prepupae and 2 pupae, 4.8 km W of Windorah, Qld, 17.iv.1969, ex dead stems of *Crotalaria.*

E. (E.) setosa

Egg.—(Fig. 43). About 1.0 mm long and 0.4 mm in maximum width; white, sausage-shaped and with a reticulate sculptural pattern (finer than that of *E. eremophila* eggs.)

First instar.—Not observed.

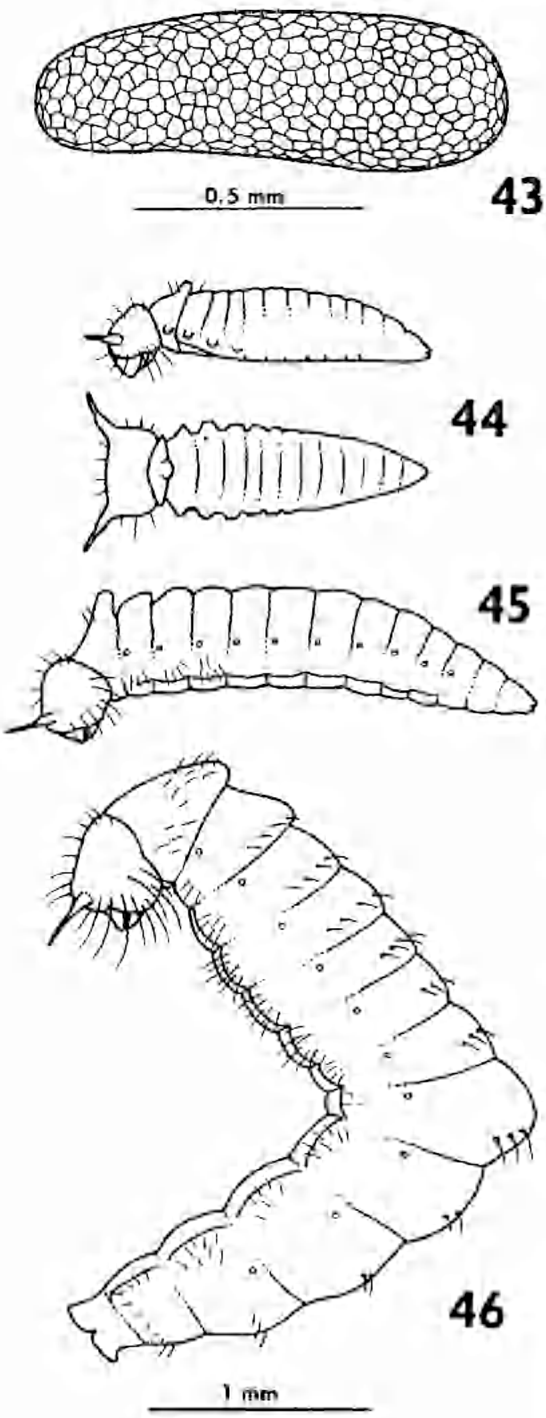
Second instar.—(Fig. 44). Similar to that of *E. eremophila* except that antennae are not capitate; 1st and 2nd body segments with a few small setae dorsally.

Third instar.—(Fig. 45). Similar to that of *E. eremophila* but with more distinct intersegmental lines and moderately developed ventrolateral body swellings. Of 4 specimens examined, 2 lacked dorsal abdominal setae and 2 slightly larger ones had setae on all but the terminal segment.

Fourth instar.—(Fig. 46). Generally similar to that of *E. eremophila* except as follows: intersegmental lines more distinct; ventrolateral swellings moderately developed; 5th abdominal segment slightly more protuberant dorsally; labial palpi situated more posteriorly on labium and further from apex.

Prepupa.—Like 4th instar but body straight and swollen anteriorly.

Pupa.—Generally similar to that of *E. eremophila* (allowing for differences correlated with



Figs 43–46. Immatures of *Exoneura* (*Exoneurella*) *setosa*. Fig. 43.— Egg. Fig. 44.—Second instar in left lateral (upper) and dorsal (lower) views. Figs 45, 46.—Third and fourth instars, respectively (left lateral views).

adult form); 3rd to 5th metasomal terga with a few short setae dorso-apically.

Material examined.—21 eggs, 32 larvae and prepupae and 12 pupae, West Beach, Adelaide, S. Aust., Feb.–Oct. 1965, ex dead stems of *Euphorbia;* 14 eggs, 28 larvae and prepupae and 3 pupae, 4.8 km N. of Peregian Beach, Qld, 9.xii.1966.

E. (E.) tridentata

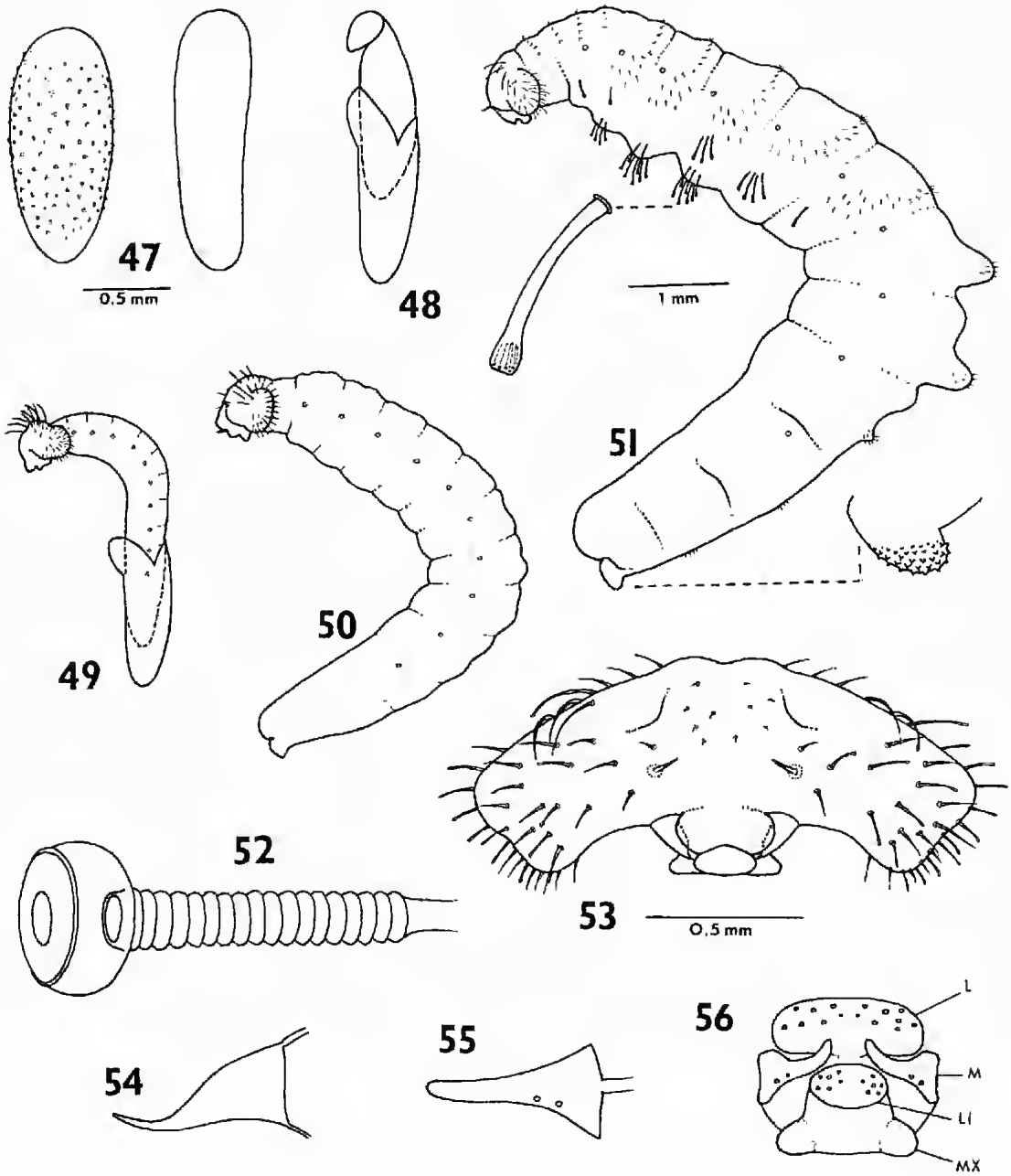
Egg.—(Fig. 47). Size variable ranging from 1.3–2.0 mm in length and 0.43–0.70 mm in maximum width; white, sausage-shaped to elongate ovoid; chorion entirely smooth to finely granular (except at the ends).

First instar.—(Fig. 48). Remains largely within chorion; head capsule smooth and appoximately circular in anterior view; antennae, mouthparts and setae absent; body sac-like without intersegmental lines, tubercles and setae.

Second instar.—(Fig. 49). Retains chorion on apex of abdomen; head broad with distinct lateral lobes which are usually reflexed against sides of prothorax; antennae absent; mouthparts developed and functional; body sausage-shaped, curved, lacking tubercles and with weak intersegmental lines; head with numerous setae, longest on vertex where they are thick throughout their length; body lacking setae.

Third instar.—(Fig. 50). Head relatively extremely broad with laterally extended lobes; antennae present, relatively short (compared with those of other *Exoneurella*) and medially directed; body curved, without tubercles (except dorso-apically on terminal segment) and with weak intersegmental lines; head with almost a complete covering of short blunt setae; body without setae.

Fourth instar.—(Figs 51-56). Head with exceptionally large quadrate lateral extensions (Fig. 53); antennae short, slender, acute and medially directed; labrum broad and bilobed with several sensoria ventrally (Fig. 56), not delimited from clypeo-frontal area; mandibles (Figs 54-56) slender, tapering and compressed apically, each with a pair of sensoria ventrally but lacking spines; labium rounded and lobe-like, bearing 2 patches of sensoria which may represent obsolescent palpi (Fig. 56); a transverse, laterally projecting lobe behind the labium probably represents degenerate maxillae (Figs 53, 56); body strongly bent at 5th abdominal segment which, like the 6th, bears a prominent dorso-median tubercle (Fig. 51); 7th abdominal segment with a small dorsal tubercle; terminal abdominal segment broad



Figs 47–56. Immatures of *Exoneura* (*Exoneurella*) *tridentata*. Fig. 47.—Eggs showing extremes of form and sculpturing. Figs 48, 49.—First and second instars with chorion attached (left lateral views). Figs 50, 51.—Third and fourth instars, respectively (left lateral views), with enlargements of capitate seta and spinose apical tubercle. Fig. 52.—Spiracle of fourth instar. Fig. 53.—Head capsule of fourth instar (anterior view). Figs 54, 55.—Left mandible of fourth instar in anterior and ventral views, respectively. Fig. 56.—Mouth parts of fourth instar (ventral view. L, labrum; LI, labium; M, mandible; MX, maxilla?). Figs 48–51 are drawn to same scale.

with a moderately large spinose tubercle just above the anus (Fig. 51); head with numerous short obtuse setae; body with short setae disposed in transverse bands on prothoracic to 4th abdominal segments and small dorsal patches on the 5th to 9th; relatively large thick capitate setae occur ventrally in clusters on the metathoracic to 2nd abdominal segments and singly or clustered laterally on the mesothoracic to 4th abdominal segments; spiracles (Fig. 52) not protruding above body wall; atrial and primary tracheal openings circular; atria subspheroidal without spines or other sculpture; subatria slender with about 18 annulations.

Prepupa.—Similar to 4th instar but body straight, swollen anteriorly and with reduced dorsal tubercles.

Pupa.—Similar to that of *E. eremophila* differing as follows. Head with fewer setae, a pair being situated low on the clypeus and several across the vertex, the more lateral ones being much longer than more medial ones; metasoma with short setae dorsally on segments 2-5 (females) and 2-6 (males) (in addition to the long lateral setae).

Material examined.—200+ eggs, 125 larvae and prepupae and 73 pupae, Lake Gilles National Park, S. Aust., 30.xii.1973–27.x.1974, ex dead stems of *Heterodendron oleifolium*.

Discussion

Regarding adult features, the 3 new species agree almost totally with the diagnosis of *Exoneurella* given by Michener (1965*b*, p. 223). The only points of disagreement relate to *E. tridentata*: in this species the eyes of males are conspicuously swollen, the apex of the 6th metasomal tergum of females is simple, not bifid, and the costal margin of the 2nd cubital cell of the fore wing of both sexes is at least as long as the 1st transverse cubital vein, not much shorter. In these respects *E. tridentata* is rather more like bees of the subgenus *Exoneura* than are other *Exoneurella*. It is also unlike its closest relatives in the constricted mandibles, angular genae, pronounced size variation and allometry of females.

Eggs of *Exoneurella* are unusual amongst those of allodapines (Michener 1973, p. 281) in having sculptured chorions. The sculpturing forms a delicate reticulum in *E. lawsoni* and *E. setosa*, fine granules in *E. tridentata* (absent in some specimens) and a combination of coarse reticulum and distinct tubercles in *E. eremophila*.

Similarities in larval form between the 4 species of *Exoneurella* correspond to similarities in adult form. Thus, larvae of *E. setosa* are most like larvae of *E. lawsoni* as described and figured by Michener (1964, pp. 422-424, figs 13-20) and larvae of *E. eremophila* differ from these 2 species in only a few minor features. On the other hand, larvae of *E. tridentata* are highly distinctive: the head capsule of 2nd to 4th instars is extraordinarily produced and quadrate laterally, the antennae are comparatively tiny, the maxillae and labium are strongly modified, 2nd instars lack lateral body tubercles but 4th instars have large dorsal tubercles on the 5th and 6th abdominal segments, spiny apical tubercles and peculiar thickened setae on the thoracic and anterior abdominal segments.

The features which will distinguish *Exoneurella* larvae from those of other groups are the following. Head capsule (of more mature instars) relatively broad with distinct hairy ventrolateral or lateral expansions; antennae (except in *E. tridentata*) of 2nd to 4th instars relatively long, slender apically, thickened basally and directed anterolaterally; no separation of clypeus and labrum; mandibles strongly tapered with slender simple apices; body of 4th instar conspicuously bent at 5th abdominal segment which protrudes dorsally; 3rd and 4th instars lacking lateral or ventrolateral extensions of body segments such as occur in other *Exoneura* (Syed 1963).

The pupae of *Exoneurella* differ from species to species in conformity with adult differences but otherwise are fairly uniform. Of the various specialized pupal structures occurring in Apoidea (Michener 1954) the only ones occuring in *Exoneurella* are long thick setae on the head and metasoma, fine short setae on the metasomal terga, and coxal spines. Michener (1964, p. 424) remarks on the absence of coxal and trochanteral spines in *E. lawsoni* but I have seen no material which could confirm this. Specific differences were noted in the number and arrangement of setae.

Exoneurella, originally established as a genus, was relegated to subgeneric status in Michener's (1965*b*) classification of Australian bees but has continued to receive generic status (Michener 1971, 1973). The taxon with its new additions remains distinctive and well defined. I consider it a purely arbitrary matter whether one recognizes it at generic or subgeneric level and have preferred to follow

Michener's (1965*b*) arrangement since it expresses the obvious affinity between *Exoneurella, Exoneura s. str.* and *Brevineura.*

Acknowledgments

I wish to thank my wife, Carol Houston, for assisting with collection of some of the material described below, Ms J. C. Cardale (ANIC) for providing some critical details of the type specimen of *Exoneura lawsoni*, and Professor C. D. Michener (KU) for advice concerning material used in his studies of *Exoneurella.*

Some of the material listed herein was collected during field work funded by the Royal Society of South Australia.

References

MICHENER, C. D. (1953).—Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. *Univ. Kans. Sci. Bull.* **35**(8), 987-1102.

MICHENER, C. D. (1954).—Observations on the pupae of bees (Hymenoptera: Apoidea). *Pan-Pacif. Ent.* **30**(1), 63-70.

MICHENER, C. D. (1963).—New Ceratinini from Australia (Hymenoptera, Apoidea). *Univ. Kans. Sci. Bull.* **49**(7), 257-261.

MICHENER, C. D. (1964).—The bionomics of *Exoneurella,* a solitary relative of *Exoneura* (Hymenoptera: Apoidea: Ceratinini). *Pacif. Insects* **6**(3), 411-426.

MICHENER, C. D. (1965a).—The life cycle and social organization of bees of the genus *Exoneura* and its parasite, *Inquilina* (Hymenoptera: Xylocopidae). *Univ. Kans. Sci. Bull.* **46**(9), 335-376.

MICHENER, C. D. (1965b).—A classification of the bees of the Australian and South Pacific regions. *Bull. Am. Mus. nat. Hist.* **130**, 1-362.

MICHENER, C. D. (1971).—Biologies of African allodapine bees (Hymenoptera, Xylocopinae). *Bull. Am. Mus. nat. Hist.* **145**(3), 219-302.

MICHENER, C. D. (1973).—Size and form of eggs of allodapine bees. *J. ent. Soc. sth Afr.* **36**(2), 281-285.

RAYMENT, T. (1946).—New bees and wasps—Part II. *Victorian Nat.* **62**, 230-236.

SMITH, F. (1854).—"Catalogue of hymenopterous insects in the collection of the British Museum. II." (British Museum: London.)

SYED, I. H. (1963).—Comparative studies of larvae of Australian ceratinine bees (Hymenoptera, Apoidea). *Univ. Kans. Sci. Bull.* **44**(8), 263-280.